

16. Interpretations of early land plant radiations: 'facile adaptationist guesswork' or reasoned speculation?

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Abstract

The diversification of higher plants following initial colonization of the land is analysed at the species level both qualitatively and quantitatively based on data from Laurussia. The overall pattern of diversification broadly parallels that described for marine invertebrates in that, following the appearance of pteridophyte-like plants (*Cooksonia*: rhyniophytoid) in the late Wenlock, numbers remained low until the end of the Silurian—early Devonian, when a proliferation of rhyniophytoids occurred. This was followed by a diversification of Zosterophyllophytina in the late Gedinian—early Siegenian, and Trimerophytina and taxa of less certain affinity later in the Lower Devonian. In the absence of direct information on habitats, of the adaptive significance (if any) of variation in individual characters, and indeed the genetic status of the 'morphospecies' involved, interpretation must be tentative. The radiation of the rhyniophytoids is evaluated as that of the archetypal founder population with presumed limited gene pool and simplicity of organization with little variation. The succeeding zosterophylls show far greater diversity in growth form and reproductive capacity, largely as a result of release from the archetypal constraints of isotomous branching and terminal sporangia seen in the majority of rhyniophytoids. The record thus supports the hypothesis of competitive replacement of

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rhyniophytoids by zosterophylls in the Gedinian, but interrelationships of higher taxa later in the Lower Devonian are less clear-cut.

Introduction

The quantitative analysis of evolutionary patterns in early vascular plants undertaken by Knoll *et al.* (1984) was both comprehensive and courageous—the latter because the data base suffers from severe shortcomings both in quantity and quality (Edwards, in press) when compared with that of marine invertebrates. Nevertheless, those authors were able to demonstrate from megafossil data that patterns of diversification, origination, and extinction fitted broadly the kinetic model for marine invertebrates proposed by Sepkoski (1979, 1981). They anticipated modification of their findings as new data became available and here, half a decade on, we propose to reconsider megafossil data for the initial phases of land colonization by pteridophyte-like plants. We incorporate in particular new information from Britain and Belgium, generously provided by Drs U. Fanning, P. Kenrick, and P. Gerrienne (Fig. 16.1). Our analysis is deliberately restricted to a limited geographical area, viz. Laurussia (broadly equivalent to the Old Red Sandstone Continent), because it is only from this region that we have the sufficiently detailed stratigraphic, sedimentological, and taphonomic background data, plus confidence in identification and correlation, that are the prerequisites for sensible interpretation. This approach does not mean that we are convinced that the 'cradle' of the higher land plants was in Laurussia. Data from Australia already indicate greater diversity (e.g. in the record of *Baragwanathia* in the Silurian, Garratt *et al.* 1984), while less well documented assemblages from the Soviet Union and China, although sometimes controversial in identification of taxa and age (Edwards 1990), will undoubtedly lead to re-evaluation on a global scale.

1. Sources of data and their temporal framework

The most satisfactory taxon used in the diversity curves is the species (Fig. 16.2). Analysis at this level is possible because of the comparatively few plants recorded and has the advantage of avoiding troublesome questions of generic/species delimitation (Edwards and Edwards 1986; Niklas *et al.* 1980, 1985). Records were taken from original papers and from research currently being undertaken in Britain and Belgium. Correlation is based on the spore zonation scheme developed by Richardson and McGregor (1986) with added data from Steemans and Streel (e.g. Streel *et al.* 1987) for Belgium, and McGregor (e.g. McGregor and Camfield 1976) for north-east America. As correla-

tion between continental/shallow marine and deeper water facies is still in its infancy, we continue to use Gedinnian and Siegenian rather than the now legitimate Lochkovian and Pragian. The choice of the absolute time-scale is subjective (see e.g. Holland 1985); we use that of McKerrow *et al.* (1985) largely because it emphasizes the relatively small and large amounts of time encompassed by Pridoli Series and Emsian Stage, respectively. The positioning of our points in relation to the absolute time-scale is also subjective. Where possible in the Lower Devonian we have divided each stage into 2–3 Ma intervals and plotted the value half-way through. In the case of the Upper Gedinnian and the Ludlow and Wenlock Series, data are recorded from the latter part, while in the Pridoli most records are early and come from just above the Ludlow Bone Bed or its equivalent.

2. Affinities of taxa

Of the three subdivisions erected by Banks (1968) from the 'psilophytes', the Zosterophyllophytina has best stood the tests of usage and additional information. It is clearly monophyletic, although its 'upper limits' *vis-à-vis* its most derived members are conjectural (Schweitzer 1983; Crane 1989). For the purposes of this analysis we exclude, as Banks did, the taxa *Baragwanathia*, *Drepanophycus*, and *Asteroxylon*. These are grouped with the Lycophytina, which is represented in the Lower Devonian of Laurussia by *Leclercqia*. The Trimerophytina with far fewer genera presents greater problems in that *Psilophyton* with a number of usually well-defined species is known both anatomically and morphologically, while *Trimerophyton* and the more complex *Pertica* lack anatomy. Particularly intriguing are the affinities of Emsian sterile plants known only from anatomy (e.g. Gensel 1984; Remy and Hass 1986b) which may well link trimerophytes and progymnosperms or iridopteridaleans. Such plants are here grouped under 'other' which also encompasses older taxa, e.g. *Estinnophyton*, *Krithodeophyton*, *Sartilmania*, *Sennicaulis*. Recent reviews of the Rhyniophytina (Edwards and Edwards 1986; Taylor 1988) emphasize just how few taxa assigned to that group are demonstrably vascular plants. This is particularly so for Silurian and earliest Devonian representatives, which are thus described as rhyniophytoid. Whether or not they form a natural taxon or are linked by convergence as a result of their morphological simplicity remains conjectural. The earliest representatives are compressions and thus lack evidence relating to the actual existence of conducting tissues or, if present, on their nature. Caution is advisable after the demonstration of moss-like conducting cells in *Aglaophyton* (*Rhynia*) *major* whose morphology typifies that of a rhyniophyte (D. S. Edwards 1986). Further, it is perhaps unreasonable

	WENLOCK	LUDLOW	PR	GEDINNIAN	SIEGENIAN	EMSIAN	EIFEL
R	Cooksonia pertoni						
R	C. cambrensis						
R	C. hemisphaerica						
R	Oval sporangium A						
R	C. caledonica						
R	Steganotheca striata						
R	Calia langii						
R	Pertonia dactyliotera		*				
R	Salopella spA		*				
R	Dyad genus A		*				
R	Tortilicaulis transvaalensis		+				
?	Psilophyrites spA		+				
Z	Zosterophyllum myretionianum						
R	Renalia spA			+			
R	Renalia spB			+			
R	Dyad genus B			+			
P	Oval sporangium B			+			
P	Oval sporangium C			+			
P	Oval sporangium D			+			
R	Salopella spB			+			
R	New genus (cf Tortilicaulis)			+			
R	Spotophyrites spA			+			
?	Psilophyrites spB			+			
R	Globose sporangium A			+			
R	Globose sporangium B			+			
Z	Z. fertile						
R	Salopella alvordii			+			
R	Isaetocarya becherovae						
R	Utriclella sparganii						
Z	Debeuvoiria splendens						
Z	Debeuvoiria sp. nov.			+			
Z	New zosterophyll genus AT1-140			+			
Z	Gomolungia brenckmeuseni						
Z	Z. cf. fertile						
Z	Stephanophyton spinosiformis						
Z	Z. rhomboid						
Z	New spiny plant Belgium			+			
Z	Extinctophyton wambroekensis						
Z	Z. planoveranum						
?	Extinctophyton confinis			+			
Z	Isaetia travençoli			+			
?	Semiothisa hippocrepiformis			+			
I	Sawdonia sp.						
Z	Thrinakophyton formosum			+			
?	Zosterophyllum bitetragonum			+			
?	Isaetocarya longisporangiate						
?	T. duntii						
Z	Gomolungia cordiformis			+			
Z	Z. cf. australicum			+			
?	Sporogonites eximius						
Z	Pabuchia regalis			+			
Z	Barbuisia dentatoloba			+			
Z	Sawdonia ornata						
?	Storkmansella langii						
I	Psilophyton thimoteense			+			
?	Platysphyllum fideipartitum			+			
R	Rhynia keyone roughensis			+			
L	Asteroxylon mackiei			+			
R	Horneophyton lichenoides			+			
?	Nodus apophyllis			+			
Z	New hairy zosterophyll keyone			+			
I	Ps. forbesii						
?	Ps. reticulatum						
?	Trileteophyton europaeum			+			
?	Diepanophyton gaspianum						
?	Psilophyton princeps						
R	Renalia buxerri						
?	Parapanatoma strobiliformis						
?	Ps. concoloratum						
?	Ps. dawsonii						
?	Ps. scabellum						
?	Karicra endygonioides						
?	Renalia graberii						
?	Equisetophyton praecox						
Z	Z. spectabile						
P	P. major						
Z	Anticophyton potanii						

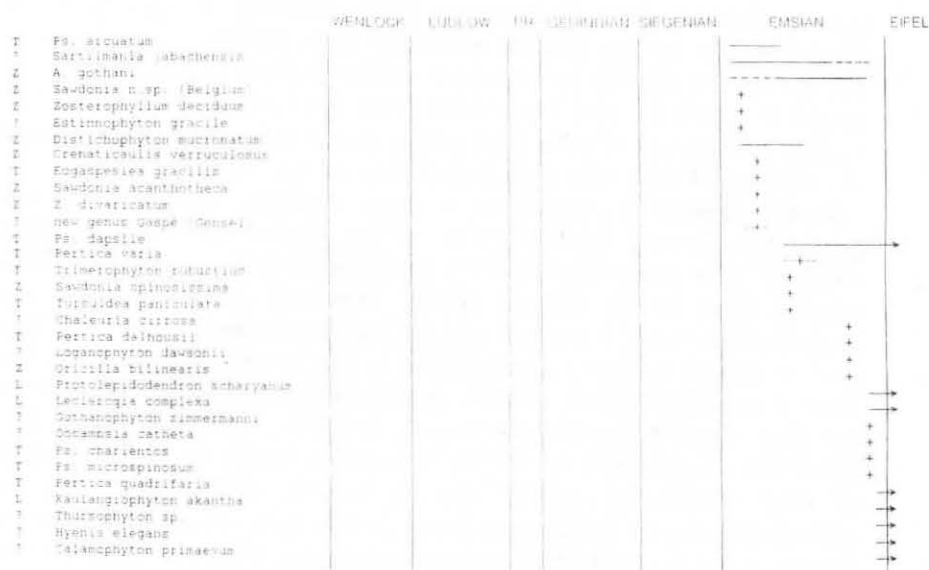


Fig. 16.1. Stratigraphic ranges of plants included in the analysis. Dashed line indicates that precise age is unknown; + represents a single record; R, Rhyniophytina/rhyniophytoid; Z, Zosterophyllophytina; T, Trimerophytina; L, Lycophytina and includes 'prelycophytes'.

to postulate that Silurian pteridophyte-like plants possessed *all* the anatomical attributes of land plants. Sequential acquisition is a possibility, beginning with 'sporopollenin'-impregnated spores, then cuticle and stomata, with evolution of tracheids following as the plants became taller (Edwards *et al.* 1986). Thus, although for this analysis we have grouped all those morphologically simple plants together, we may well be dealing with a radiation of a number of higher taxa, and whether or not these were monophyletic remains to be resolved.

3. The missing data

The megafossil record is dominated by fragments of aerial sporophytes while convincing examples of independent gametophytes, as anticipated from their homospority, are very few. Low fossilization potential, as deduced from the parenchymatous construction, and lack of homoiohydric attributes of extant representatives may explain this. However, the most acceptable records—*Lyonophyton* and an unnamed form (Remy 1982; Remy and Hass 1986a), both from the Rhynie Chert—possessed cuticles and conducting tissues, as did the more

equivocal *Sciadophyton* (Schweitzer 1983). Whether or not these are typical awaits the recognition of further gametophytes in clastic sediments, but the present lack of direct evidence should not be used as an excuse to ignore the relevance of this generation to considerations on the ecology and spread of early land plants, nor to overlook the significance of its haploidy when discussing evolutionary processes.

In the haploid gametophyte recessive mutants, pertaining to that generation, would be expressed in the phenotype. A favourable recessive trait might thus become established in the population more quickly than in the diploid phase. However, selection would act immediately on a new mutant and the long-term advantage of a hidden pool of genetic resources maintained in the heterozygous state in the diploid would not occur. Further gene expression is clearly different in the two generations and phenotypic features, both anatomical and physiological, selected for in one generation might be disadvantaged or even eliminated in the next if linked, either genetically or physiologically, to a deleterious trait in that generation. Such contradictory selection in the two generations might delay considerably the fixation of advantageous characters compared to organisms not showing alternation of independent generations, and selection would favour the loosening or breaking of linkage between favourable traits in one generation and disadvantageous traits in the other. Similarly, any mechanism that would result in closer linkage between advantageous characters in the gametophytic and sporophytic generations respectively (e.g. chromosome inversions) might be favoured.

Although habitats (see p. 357) remain conjectural it seems reasonable to assume that the water requirements and water dependence of early pteridophyte gametophytes were similar to those of extant forms, and that they colonized damp habitats. Thus, attainment of reproductive maturity in drying environments would have been favoured by rapid germination under favourable conditions, physiological desiccation tolerance, and speed of reaching maturity, and there may well have been intense inter- and intraspecific competition for water, light, and scarce nutrients (Beerbower 1985) during vegetative growth. It now seems unrealistic to postulate that the pioneering pteridophytes colonized almost 'empty' land surfaces, and indirect evidence points to an existing ground cover of thalloid organisms (Gray 1985*a, b*; Selden and Edwards 1989; Strother 1988). Competition between this and the early pteridophyte gametophyte may well have been intense and initially successful sexual reproduction low. This in turn may give a partial explanation for the time-lag illustrated in Fig. 16.3 (see also Jablonski and Bottjer, Chapter 2, this volume).

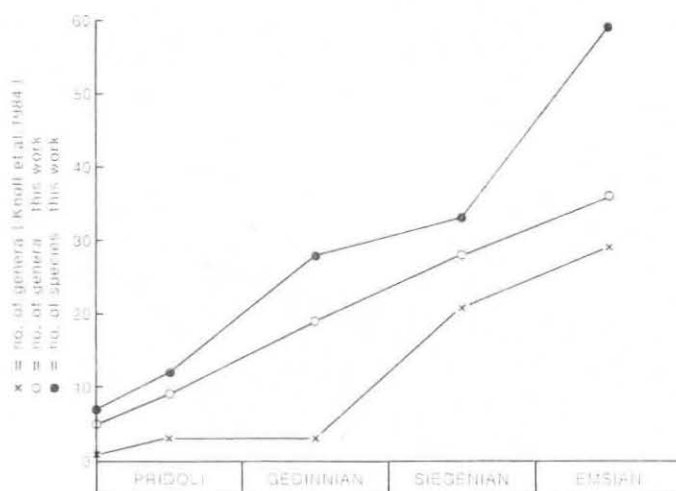


Fig. 16.2. Total numbers of late Silurian/early Devonian species and genera from this analysis plotted on the graph for generic richness produced by Knoll *et al.* (1984).

4. Habitats

All Silurian megafossils are recovered from marine sediments and give no clues to the habitats of the living plants. Most workers favour moist environments at the terrestrial-freshwater interface (Selden and Edwards 1989; but see Schweitzer 1983). Since latest Silurian records are in marginal marine and early Devonian records in fluvial sediments, coastal plain communities in a variety of habitats seem likely. Such habitats would include mudflats, dune slacks, and stream-, river-, and lake-sides and are all classified as variable in time and space. This environmental variability would act as a disruptive selective force with the net effect of increasing the range of genetic diversity within early land plants, in that different phenotypes would have optimal fitness in the different microenvironments. On the other hand extremely disturbed environments (e.g. those subjected to regular flooding) would be unlikely habitats in that there would have been no opportunity for the buildup of nutrient- and water-retentive soil, the preferred substrate for the establishment of higher plants (Beerbower 1985).

Presentation of data

1. Ranges of species are given in Fig. 16.1. A comprehensive bibliography is impossible in the space allocated, but will be included

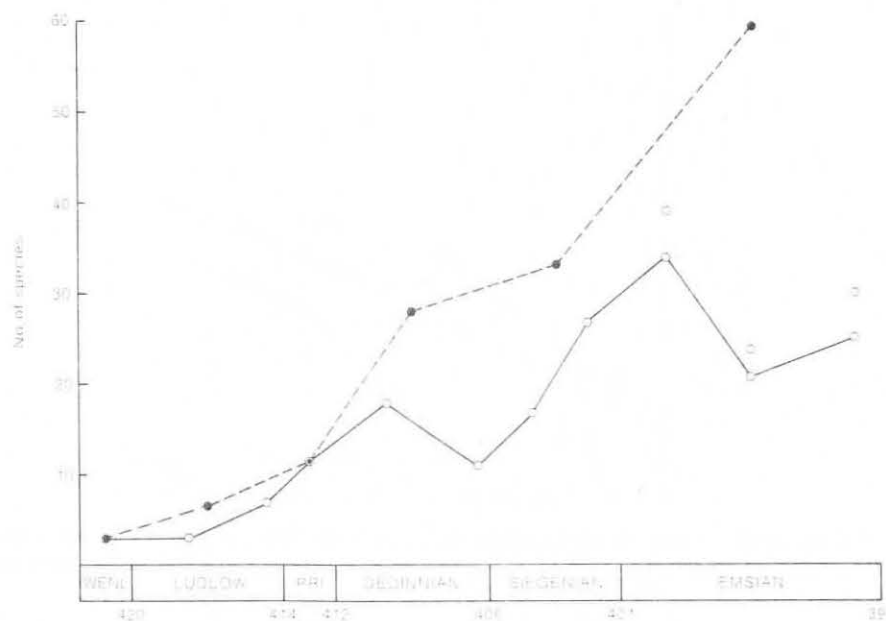


Fig. 16.3. Plot of numbers of species present in the upper Silurian and Lower Devonian. Interrupted lines join points (solid circles) for total number within the series or stage. Circles not connected by lines are possible maximum numbers of species within the Emsian.

in a paper being prepared with colleagues from Liège. This will give a more detailed stratigraphic column and information on localities.

- Numbers of species and genera are expressed graphically in Figs 16.2 and 16.3. Note that when *totals* for series and stages are plotted (Fig. 16.2) the shape of the curve broadly parallels that produced by Knoll *et al.* (1984). A more accurate picture is obtained by subdivision into 2 or 3 Ma intervals. Origination and extinction rates have not been calculated because of the high percentage of single records (cf. Niklas *et al.* 1985). These are indicated in Fig. 16.1 by '+' symbols.

Radiation of rhyniophytoids

1. Quantitative overview

All fertile Laurussian Silurian records are of rhyniophytoids; the first zosterophyll is recorded in the early Gedinian. The increase in number of species in the graph thus documents a radiation of rhyniophytoids,

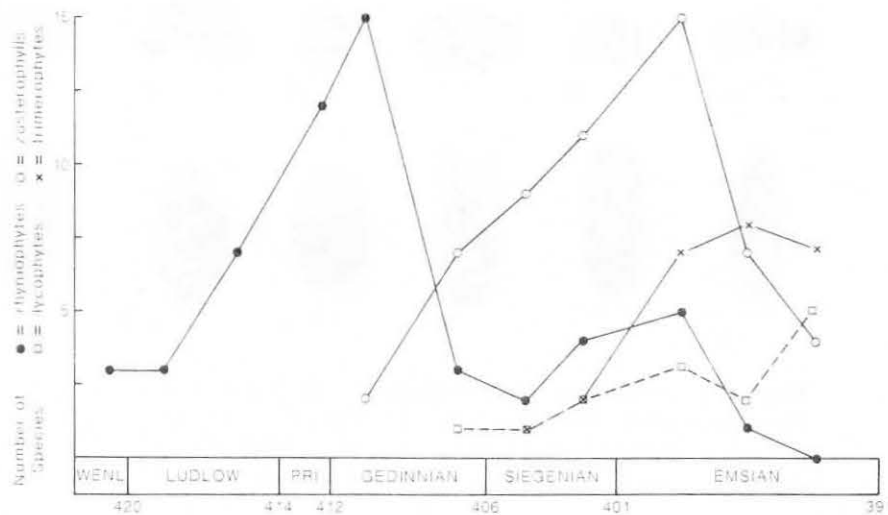


Fig. 16.4. Changes in diversity at the species level of subdivisions present in the late Silurian and early Devonian. Species of uncertain affinity are excluded.

and shows slow increase in Wenlock and Ludlow times followed by diversification in the Pridoli and early Gedinian (Fig. 16.4). This parallels the pattern described by Knoll *et al.* (1984) except that the lag phase occurs earlier in the Silurian. Rhyniophytoids/rhyniophytes quite rapidly decline in species number in the Siegenian and latest Emsian, with minor recovery in between, although the affinities of younger examples are conjectural (see p. 363).

2. Qualitative analysis of variation

Rhyniophytoids are remarkably similar in overall morphology: isotomously branched, usually smooth, axes are terminated by solitary homosporous sporangia, their shape (globose, reniform, discoidal, fusiform) providing the major source of variation (see Fig. 16.5). On the basis of *in situ* spore studies branched sporangia originally thought to be new taxa (Edwards and Fanning 1985) are now known to be variants of oval or fusiform kinds (e.g. *Salopella*). Most of the sporangia are smooth, but two recently described genera bear prominent projections (Fanning *et al.* 1990, in press). Thickened distal sporangial margins (e.g. as in *Cooksonia caledonica*) evince predetermined dehiscence, but such anatomical modifications are not common in early rhyniophytoids. The isolation of spores from a large number of taxa (Edwards *et al.*, in press) has provided further characters for taxon delimitation and indicates the

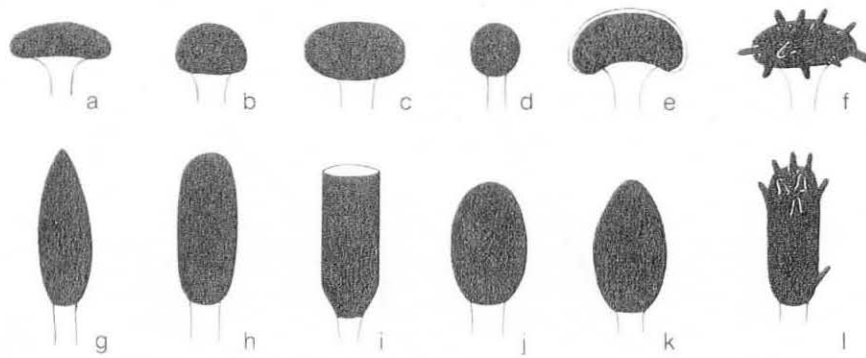


Fig. 16.5. Silhouettes of sporangia of late Silurian and basal Devonian rhyniophytoids to demonstrate morphological diversity. Drawings not to scale: a, *Cooksonia pertoni*; b, *C. hemisphaerica*; c, d, *C. cambrensis*; e, *C. calidonica*; f, new genus; g, *Salopella*; h, j, k, unnamed taxa; i, *Steganotheca*; l, *Caia*.

existence of more species than is apparent from morphology alone. We have incorporated this information into our data base (Fig. 16.1), although many of the taxa are not yet formally described.

Gedinnian rhyniophytoids, although slightly more numerous, show little morphological advancement on Silurian representatives. More complex branching is recorded, the most important type being a departure from isotomous branching by overtopping. Axes are usually smooth. Exceptions include sterile axes with triangular projections from the Pridoli of Dyfed and those with short spines from the Gedinnian of Targrove (Edwards and Fanning 1985, plate 1, fig. 14) but their affinities are obscure. Siegenian rhyniophytes are more complex; the most completely known come from the Rhynie Chert, e.g. *Rhynia gwynne-vaughanii* and possibly *Horneophyton*. Only in the latter is there a clear demonstration of centrarch xylem. The relatively undifferentiated sporangia in *R. gwynne-vaughanii* were abscised from a branching system with more sophisticated growth patterns (D. S. Edwards 1980). In contrast, in the recently described *Uskiella*, branching is conservative but sporangia possessed anatomical modifications for predetermined dehiscence (Shute and Edwards 1989). The remaining putative rhyniophytes are known only from impressions or compressions. The most controversial Emsian example, *Renalia*, has a very well-defined pseudomonopodial branching system, and reniform sporangia with marginal dehiscence terminating lateral branch systems (Gensel 1976). A number of taxa here recorded as 'other' are sometimes considered to be possible intermediates between rhyniophytes and other taxa, but again anatomical evidence is lacking.

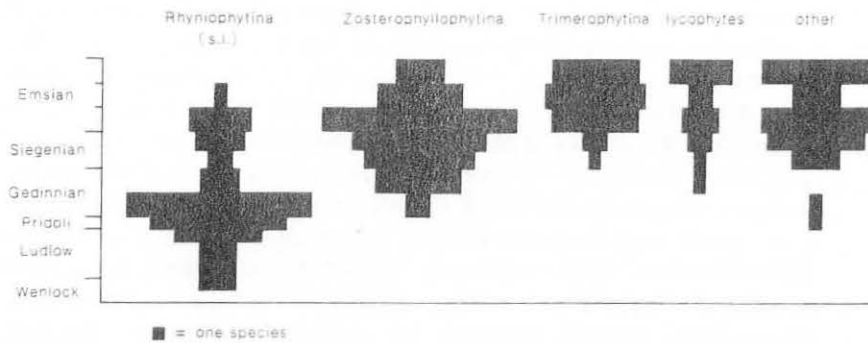


Fig. 16.6. Numbers of Silurian and Lower Devonian species plotted according to affinity.

3. Analysis and explanation of pattern

The nature of the megafossil record in the Silurian raises the possibility that the lag in diversification in the Ludlow results from a combination of taphonomic bias and ignorance. All records are in marine sediments (Richardson and Edwards 1989), but the older plants were transported farther and buried in deeper water, while Pridoli examples were preserved closer to the shore and thus perhaps better represent the composition of (coeval) terrestrial vegetation. Greater diversity is seen in Gedinian assemblages preserved in fluvial sediments. Older records also contain fewer specimens. Thus facies bias undoubtedly contributes to the lag phase, but Ludlow and Wenlock records from more marginal facies are needed to assess its extent. The dispersed spore record which is more independent of facies shows a similar pattern, but its analysis is beyond the scope of this chapter (Richardson and Burgess, in progress).

Anatomical data are rare in pre-Pridoli fossils and taxon delimitation is based solely on morphology. We have shown already that sporangia of Silurian *Cooksonia pertoni* contain two kinds of spores (Fanning *et al.* 1988) and that this situation is paralleled in fusiform (*Salopella*-like) and oval sporangia (Edwards *et al.*, in press). We have taken this sort of information into account when compiling Pridoli and Gedinian lists, but have no relevant data on pre-Pridoli rhyniophytoids. A further source of cryptic diversity, but not yet identified in the Silurian, relates to the nature of conducting cells—*Aglaophyton* and *Rhynia* might well be reunited if known only as compressions! We thus have little doubt that Silurian numbers are underestimates but also question that inadequacies of preservation and recognition are entirely responsible. We consider it possible that there was an initial period when the pioneering land plants, having attained or being in the process of

evolving the anatomical and biochemical sporophytic attributes essential for homoiohydric and being subjected to intense competition of gametophytes (p. 356), were struggling to maintain a foothold in terrestrial ecosystems. Thus there would have been a period of increasing physiological fine-tuning, when numbers of individuals may well have been low. Using the terminology of modern population ecology, these were small isolated founder populations with very limited gene pools and perhaps lacking potential for major morphological diversification. This tendency would be amplified by archetypal constraints, in particular those relating to isotomous branching and determinate growth imposed by terminal sporangia. Indeed, the proliferation of taxa recorded at the end of the Silurian results overwhelmingly from variation in sporangial and spore characters and provides little evidence for release from these archetypal constraints.

It is tempting to describe the late Silurian increase as an adaptive radiation, but this presupposes knowledge of plant habitats and the functional morphology and hence adaptive significance of the innovations involved. Three examples are given to illustrate the type of reasoning involved.

1. *Exine ornamentation.* The significance of exine structure has been extensively debated elsewhere (e.g. Chaloner 1976) and has been related to buoyancy, defence, lodging, and timing of germination. The significance and relative merits of different kinds of ornament (con, verrucae, spinae, etc.) is even more controversial. We have evidence of certain trends in different lineages (Fanning *et al.* 1988), suggesting convergence in response to similar selective pressures (e.g. those resulting from colonization of increasingly drier habitats), or perhaps to developmental constraints, but the fact remains that a wide range of similar morphologies is present in both the Silurian and early Devonian, although with increase in diversity in the latter.

2. *Anatomical modification for predetermined dehiscence.* A distinctive sporangial border characterizes a small number of late Silurian rhyniophytoids, and work in progress in Cardiff indicates cellular differentiation in this area. Such predetermined dehiscence ensures that the maximum number of spores are exposed on splitting into two equal valves and raises the possibility of control over timing of dehiscence. Similar modifications are much commoner in early Gedinian isolated terminal sporangia and, of course, characterize the zosterophylls.

3. *Emergences on axes and sporangia.* Axial spines may have had photosynthetic or protective functions (e.g. Kevan *et al.* 1975). They are

rare in the Silurian and only slightly less so in the early Devonian. The recent demonstration of prominent sporangial projections in two Pridoli taxa prompted speculation on their functions, in nutrition, defence, and prevention of desiccation (Fanning *et al.* 1990, in press).

All these deliberations are based on small fragments of the aerial parts of plants and we are mindful of Professor J. Harper's condemnation as 'facile adaptationist guesswork' of the practice by ecologists working on extant vegetation of searching for interpretations on any isolated part of an organism and giving it an explanation as an optimal system (Harper 1982, p. 17). His comment is even more salutary for palaeobotanists, where there is no chance of evaluating the sets of compromises that are inevitable in the partitioning of resources between, for example, aerial vegetative growth, acquisition of mineral resources, and reproductive capacity. It has been suggested that such plants are an early example of r selection with allocation of assimilate to spore production and less to production of axes, although this 'strategy' would have placed them at a disadvantage for dispersal and light harvesting. It has also been argued that such continuously unproductive environments produce 'adversity selection' (Whittaker 1975) and favour individuals that make smaller demands on scarce environmental resources and thus are likely to be slower growing and have low reproductive effort (Grime and Hodgson 1987). Here, admittedly at the threshold, rather than the product of long-term selection pressures, we are dealing with plants showing reduction in both vegetative and reproductive vigour in response to putatively poor environmental conditions. Certainly in considering Siegenian to Emsian rhyniophytes growing in presumably ameliorating substrate there appears to be no marked increase (even in *Renalia*) in sporangial/spore production relative to 'length' of axis (although this needs quantifying). Instead, selective pressures produced increased height or sophistication of dehiscence. Increase in efficiency of capture and recycling of scarce mineral nutrient resources by many extant plants growing in unproductive habitats is achieved by mutualistic associations, e.g. lichens and mycorrhizal-root associations. It has been postulated that associations between algae and aquatic fungi were the forerunners of mutualistic associations between early land plants and fungi, conferring on these plants a greater resistance to desiccation and a greater efficiency of capturing scarce mineral nutrients (Pirozynski and Malloch 1975).

Finally, each isolated population represents a different genetic resource in terms of the mutants and recombinants it contains. The direction and magnitude of evolutionary change in response to a particular selective pressure will be constrained by the genetic

variability available and thus may well differ between populations. In each population the evolutionary response would be 'along the line of least resistance' (Stebbins 1970, p. 320) and would not necessarily be the optimum response to that particular environmental change. Thus we cannot conclude that features we observe in organisms represent optimum responses and adaptations to past selective forces and environments. Indeed, it is possible that some diversity of characters may not have arisen as a result of adaptive responses to differing selection pressures but may be the result of association with unknown physiological or morphological adaptive features caused by pleiotropy or genetic linkage (linkage disequilibrium). The search for adaptationist explanations for each trait may also be confounded by oversimplified concepts of environmental factors. Natural selection forces are most often considered in terms of physical and chemical measures of the environment but powerful selection on plant populations may operate via biotic forces, including competition from neighbours, herbivory, and parasitism. Such factors may be extremely complex and vary over very short distances resulting in considerable effective heterogeneity in environments which are seemingly uniform in terms of physical and chemical parameters (e.g. Burdon 1980; Harper 1982). Such 'Sisyphean' forces may also result in coadaptation and coevolution between neighbours, both between and within species. Therefore we should be aware of the dangers of underestimating the great diversity of selective forces acting upon plant populations and of trying to produce 'adaptationist' explanations for every character variant.

Vegetation in the late Silurian and early Devonian

We can envisage late Silurian and early Devonian rhyniophytoid-dominated communities forming 'mixed turfs', tens of millimetres in height, exploiting a variety of microenvironments maintained by ever-changing physical and biological factors. As a result of inter- and intraspecific competition morphotypes may have gained temporary advantage, but such ephemeral dominance is impossible to identify in the geological record; our evidence comes from a very small number of horizons. In the Gedinnian there was a general increase in size and height with some overtopping, a release from isotomous branching constraints. In addition, the first records of *Zosterophyllum* indicate the capacity of clonal growth and hence local dominance, for which we have no direct evidence in the Silurian of Laurussia.

Radiation of Zosterophyllophytina

1. Quantitative overview

The Laurussian zosterophylls appear near the base of the Devonian, show major proliferation at the end of the Gedinnian and early Siegenian, and begin to decline in the mid-Emsian. The final record is in the upper Devonian. When compared with the rhyniophytoids there is no pronounced lag between origin and diversification. Examination of raw numbers of early and late Gedinnian species in Fig. 16.3 fails to reveal the striking change in affinity of the taxa involved (Figs 16.4 and 16.6). Early Gedinnian assemblages, where numbers are somewhat inflated by our current research on two Dittonian localities in the Welsh Borderland, are predominantly rhyniophytoids, whereas in the uppermost Gedinnian zosterophylls are more numerous.

2. Qualitative analysis of variation

The proliferation of zosterophylls in the late Gedinnian and early Siegenian produced almost all the variation known in the group. Later innovations include asymmetry in sporangial dehiscence and solitary sporangia. The uniting features of zosterophylls are a substantial/prominent exarch xylem strand and lateral sporangia in which height rarely exceeds breadth and which split in a predetermined way into two valves. Variation exists in the distribution of sporangia, sporangial orientation and symmetry of dehiscence, branching patterns, and presence or absence of emergences (see e.g. Kenrick and Edwards 1988; Edwards *et al.* 1989; Niklas and Banks 1990; Fig. 16.7). The earliest member, *Zosterophyllum*, possessed a terminal strobilus (or spike) of sporangia which are spirally inserted in *Z. myretonianum*, and borne in two rows in the slightly younger *Z. fertile*. Such organization clearly increases the sporing capacity of these plants when compared with rhyniophytoids, while basipetal maturation ensured spore production over a longer period (Edwards 1975), and anatomical differentiation related to sporangial dehiscence may have afforded additional control over the timing of dispersal. The K- and H-configurations recorded in vegetative branches of *Z. myretonianum* and a number of other species are believed to be concentrated in the basal regions of the plants and to have resulted in a tufted or creeping growth form, with a number of strobili produced by the same plant (Gerrienne 1988). The extent of such clonal behaviour remains unknown but, in that a single plant had the potential to cover a considerable area, it could have cut down inter- and intraspecific competition. Tiffney and Niklas (1985) postulated that such prolonged vegetative development would also have reduced reliance on more risky sexual reproduction.



Shortage of space precludes a comprehensive description of zosterophyll diversity; we concentrate on just four aspects and somewhat hesitatingly (see p. 363) speculate on any adaptive significance.

1. *Orientation of sporangia.* In the ancestral and commonest condition exemplified by *Zosterophyllum*, sporangia are held upright on short stalks and split so that one valve (the adaxial) is close to the axis. In the orientation that characterizes *Gosslingia*, the subtending stalks are at right angles to the strobilus axis and the sporangium splits into right and left valves which are capable of unrestricted opening when compared with the *Zosterophyllum*-type where movement of the adaxial valve could have been restricted by the strobilus axis. We know nothing about the ontogeny of *Gosslingia*-type except that it is frequently associated with circinate tips (Niklas and Banks 1990). However, the orientation of the *Zosterophyllum*-type is clearly an advantage during the development of a strobilus where older sporangia overlap and could protect younger sporangia.

2. *Distribution of sporangia.* This ranges from compact to lax strobili, to examples where sporangia are more widely distributed, perhaps occasionally forming more defined zones. In the latter there is sometimes quite a precise relationship to branching (e.g. *Gosslingia*, Edwards 1970; *Tarella*, Edwards and Kenrick 1986). As mentioned earlier, more extensive distribution of sporangia increases duration of spore production, an attribute which in the later Carboniferous lycophytes (DiMichele and Phillips 1985) has been related to colonization of disturbed habitats. It would also spread temporally the energy demand of sporangium and spore production. A terminal strobilus may well have imposed a considerable drain on the photosynthetic resources of the erect axis; the extent to which the basal ramifying axes were exposed is conjectural (Walton 1964). It would also have necessitated efficient conducting tissue, and the size of the zosterophyll strand, which is comparatively large when compared with that in rhyniophytes, may have initially evolved in response to the requirements of the strobilus sink. We have no evidence for amounts of phloem, but it would presumably have formed a correspondingly more extensive layer around the xylem. Such speculation may well (and justly) be cited as an

Fig. 16.7. Reconstructions of representative late Gedinian/early Siegenian zosterophylls. a, *Thrinophyton*; b, *Gosslingia*; c, *Zosterophyllum myretonianum*; d, *Z. fertile*; e, hypothetical reconstructed basal regions of a *Zosterophyllum*; f, *Deheubarthia* (spines omitted); g, part of vegetative axis of *Deheubarthia* with spines; h, *Tarella*.

excellent example of the oversimplistic approach (see p. 363) especially as we have, for example, no good comparative evidence for three-dimensional xylem from rhyniophytes outside the Rhynie Chert which may represent an atypical environment.

Staggering of sporangial development would thus have spread energy demands of spore production, and perhaps increased sporing capacity. Despite limitation of the data set it would be interesting to compare the number of sporangia per unit volume of axis in the more completely known zosterophylls. The most inefficient in terms of productivity would undoubtedly be Emsian *Koniora* where a solitary sporangium occurs below a branch point (Zdebska 1982). Here it is tempting to suggest that energy resources were diverted into production of numerous spines!

3. *Symmetry in branching.* One of the most remarkable features of a number of zosterophylls is the planar nature of the aerial, presumed upright, branching system. Bilateral symmetry in sporangial arrangement (viz. the two-rowed strobilus of *Z. fertile*) was already established early in zosterophyll evolution and, in the late Gedinnian, lateral branches were alternately produced on opposite sides of the axis such that the overall system was in one plane (*Gosslingia*, *Deheubarthia*). Similarly organized plants are also recorded in the Siegenian (*Thrinakophyton*, *Sawdonia*). In isolation such a flattened system would surely have been readily blown over but, in that we have some evidence for monospecific stands in, for example, *Gosslingia breconensis* and *Tarella trowenii* in the early Siegenian, it is possible that, when associated with clonal growth, such branch systems may have allowed closer packing with less mutual interference and hence more efficient light harvesting.

4. *Plasticity in branching.* Phenotypic plasticity in the vegetative phase would have been advantageous in plants growing in disturbed habitats, and this may have been achieved, at least in part, by the lateral projections present in certain zosterophylls, which are not part of the main branching system, but show varying degrees of development. Most common are prominent elevations occurring just below a branching point (axillary tubercles/subaxillary projections, e.g. Edwards *et al.* 1989) which may well be analagous to the rhizophores in extant *Selaginella* where they usually function as roots, but can develop into leafy shoots on damage to growing points. Thus in late Gedinnian–Siegenian *Deheubarthia splendens* downwardly directed spiny branches occur in the subaxillary position and in Emsian *Crenaticaulis verruculosus*, in which aerial axes possess two rows of tooth-like enations, similarly placed branches are smooth. In both taxa more work is needed

to determine the extent of development of such branches, and of their morphological variability. In early Siegenian *Tarella trowenii*, more randomly placed projections range from short-coiled or hooked structures, reminiscent of circinate tips, to more extended branched axes and it was suggested by Edwards and Kenrick (1986) that these were dormant 'buds' capable of developing following partial burial or 'uprooting' of the plants, during flooding. Finally, in *Sawdonia ornata* the small projection on the abaxial surface of a lateral branch close to its departure was interpreted as a possible dormant 'root-like' primordium in the planar aerial system (Rayner 1983).

Vegetational change in the Gedinnian-early Siegenian

The rhyniophyte-dominated coastal plain vegetation of southern Britain persisted into the Gedinnian but the 'turf' was taller and there were occasional stands of *Zosterophyllum*. In contrast, coeval assemblages preserved in the internal facies of the Old Red Sandstone of Scotland were dominated by *Z. myretonianum* and the almost monotypic vegetation in the vicinity of lakes and rivers was thus taller (tens of centimetres) and both vegetatively and reproductively more productive.

A recent attempt at interpretation taking into account taphonomic biases (Edwards 1990) found some evidence for regional differences in vegetation, but whether or not this resulted from failure of the rhyniophytoids to migrate further inland or that they had, and were subsequently ousted by *Zosterophyllum*, cannot be determined. The second explanation (i.e. competitive replacement) is far more likely for the late Gedinnian-early Siegenian radiation of zosterophylls. In the previous section we have emphasized those innovations which appear to increase the vigour and fitness of the plants in terms of greater height-prolonged vegetative growth and increased ground cover, more sophisticated controls over dispersal, and increased reproductive capacity. Whether or not these plants were able to colonize a wider range of environments, perhaps drier or less stable, remains conjectural. Clearly, they would still be limited to damp places by the constraints of the homosporous pteridophyte life cycle, although it had been suggested that extensive clonal growth would reduce dependence on sexual reproduction. In addition, *Sciadophyton*, a probable gametophyte, and possibly that of *Zosterophyllum*, may have possessed homoiohydric characters.

There remains the possibility that, because the facies in which the older rhyniophytoids occur are not so frequent from the late Gedinnian onwards, such plants existed but were not preserved. Detailed quantitative analysis of dispersed spore assemblages considered in conjunction

with the rapidly increasing data base on *in situ* spores may eventually resolve the problem. Current megafossil evidence indicates that a few rhyniophytes survived the *Zosterophyllum* competition and these possessed derived characters in branching pattern (e.g. in Emsian *Renalia*), and/or dehiscence mechanisms (e.g. *Renalia* and *Uskiella*).

Vegetational change in the mid-Siegenian-Emsian

Both lack of space and familiarity with the raw data preclude extensive treatment here. The best Siegenian and early Emsian records come from mainland Europe (e.g. Gerrienne 1983; Schweitzer 1983; Stockmans 1940) while the most complete record throughout the Emsian derives from the north-eastern seaboard of North America (see e.g. Gensel and Andrews 1984). However, detailed numerical analysis is hampered because some taxa (e.g. *Baragwanathia abitibiensis* from the Sextant Formation of northern Ontario, Richardson and McGregor 1986, and *Koniora andrychoviensis*, Zdebska 1982) cannot be precisely located within the Emsian. As yet there is little well-founded evidence for provincialism; differences probably reflect the patchy nature of the record. Thus, for example, research on early Emsian assemblages from Belgium (Gerrienne 1983) demonstrated the presence, for the first time in Europe, of a number of North American taxa.

Analysis of the taxonomic composition of late Siegenian/early Emsian assemblages is complicated by the high percentage of taxa that lack sufficient diagnostic anatomical characters for identification and/or present new combinations that cannot readily be accommodated in existing classifications (e.g. *Estinnophyton*, *Sartilmania*), some of which may be advanced rhyniophytes or even transitional between trimerophytes and 'ferns' or progymnosperms (Gensel 1984). Such taxa are included under 'others' in Figs 16.4 and 16.6.

Whereas this analysis has strongly supported Knoll's (1986a) hypothesis that rhyniophytes were competitively replaced by zosterophylls, his contention that zosterophylls and lycophytes were replaced as principal contributors to infloreal diversity by trimerophytes receives only limited quantitative support at the species level. Trimerophytes (first recorded in Laurussia as *Dawsonites* sp. (Croft and Lang 1942) early in the Siegenian) began to diversify at the beginning of the Emsian, when zosterophylls reached maximum species diversity. The greater number of zosterophyll genera reflects the fact that they are based on a variety of combinations of vegetative and sporangial characteristics (see discussion in Edwards *et al.* 1989). In contrast, proliferation of trimerophytes largely results from the increase in the number of species of *Psilophyton*, where gross morphology and lateral branches with

trusses of elongate sporangia are conservative generic characteristics.

There is thus no clear-cut picture of one group rising to dominance and replacing another. What is evident, as Knoll (1986a) noted, is that successively younger taxa tend to be larger in all dimensions and are far more complex morphologically (although still based primarily on axial branching systems) and that taxa must have had increased capacity for harvesting light, and absorbing and transporting water and nutrients (Knoll 1986a, p. 139) and also, particularly in the case of trimerophytes, increased capacity for spore reproduction.

Towards the end of the Lower Devonian zosterophylls existed alongside the trimerophytes but their decline in numbers was associated with the appearance of taxa usually found in the Middle Devonian (e.g. *Calamophyton*, *Leclercqia*) and others of less certain affinity which show innovation in reproductive (*Chaleuria*, Andrews *et al.* 1974) and vegetative (*Gothanophyton*, Remy and Hass 1986b) characters.

Schweitzer (1983) presented a detailed ecological setting for Rhenish Lower Devonian land plants with monotypic swards or 'meadows' growing at various levels in the littoral zone including intertidal and salt marsh. The most extensive review of vegetation towards the end of the Devonian centres on Gaspé and Maine assemblages (Andrews *et al.* 1977; Gensel and Andrews 1984; Kasper *et al.* 1988). Based on sedimentological studies and the predominant occurrence of monotypic assemblages, these authors reconstruct a coastal low-lying marshland colonized by dense monospecific stands of tall trimerophytes interspersed with mats of zosterophylls and (pre)lycophytes with more pronounced rhizomatous growth and occasional upright shoots. Distribution of taxa was perhaps controlled by small-scale topographical features associated with differences in soil moisture.

Apologia

It is undeniable that, in the quantitative analysis of raw data leading to attempts at elucidation of evolutionary patterns and processes in the fossil record, palaeobotany lags well behind invertebrate palaeontology, although recent analyses by North American workers (e.g. Niklas *et al.* 1980, 1985; Knoll *et al.* 1984; Knoll 1986b) are beginning to rectify the balance. Detailed assessments of diversification of early land plants as reported here flounder due to incompleteness of the terrestrial record and the fragmentary and unproductive nature of the megafossils themselves. Our perhaps excessive caution in handling the raw data has been matched or even negated by our lack of caution in our overly optimistic and imaginative attempts to ascribe adaptive significance to all morphological variation, especially since our knowledge of the nature

and diversity of the physical, chemical, and biotic environment which these early land plants inhabited is so rudimentary.

To overemphasize the limitations of the data base on early land plants and their environment, as done yet again here, may seem defeatist, but we are slightly encouraged in this approach by the demonstration of similar difficulties encountered in explaining character diversity in extant vegetation.

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